Three New Species of the *Pagurus lepidus* Complex (Decapoda, Anomura, Paguridae) from the Eastern Pacific

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ABSTRACT. Three new species reported as *Pagurus lepidus* (Bouvier), or included in the *Pagurus lepidus* complex by the senior author in earlier publications, are now described and illustrated. *Pagurus rhabdotus* appears to be endemic to the outer coast of the Baja California peninsula and *Pagurus nanodes* is known only from Central and northern South America, whereas *Pagurus virgulatus* has a broad geographic range from central Mexico to Ecuador. *Pagurus rhabdotus* and *P. virgulatus,* like *P. lepidus,* possess the striped ambulatory legs so typical of most of the *provenzanoi* group species. In contrast, *P. nanodes* is distinctive in having banded walking legs.

INTRODUCTION

The Gulf of California, Mexico, more popularly referred to as the "Sea of Cortez" (Steinbeck and Ricketts, 1941), has been an area of carcinological interest for more than a century. The early "Albatross" expeditions of the late 1880s (cf. Townsend, 1901) provided much of the material upon which Benedict (1892) based his descriptions of new pagurid species from the Gulf. The fauna of the Gulf and west coast of Baja ("Lower") California was investigated in the 1930s by the Templeton Crocker Expedition ("Zaca", New York Zoological Society) (Beebe, 1937; Glassell, 1937) and in the 1930s and early 1940s by the Allan Hancock Foundation ("Velero III," University of Southern California) (Fraser, 1943). The outer coast of the Baja California peninsula was also the focus of the 1964 "Magbay" Expedition (cf. Haig et al., 1970). More recently, Brusca (1973, 1980) provided a summation of 24 months of field collecting in the Gulf. Hermit crabs have also been included in numerous reports of decapods from Central and South America (e.g., Rathbun, 1910; Boone, 1931; Holthuis, 1954; Bott, 1955; Del Solar et al., 1970). However, few species of *Pagurus* have received more than brief attention. Ball and Haig (1974) reported that of the 27 species of hermit crabs collected during the 1968 Stanford Oceanographic Expedition's survey of the intertidal and shallow subtidal regions from Paita, Peru to Bahía Magdalena, Baja California, Mexico ("Te Vega" Expedition 18), only nine were pagurids and seven of those represented species of the *provenzanoi* group. Although the authors indicated that these latter species would be treated separately, the report they had planned was never completed.

Since the description of *Pagurus lepidus* (Bouvier, 1898), virtually all small pagurid species from the Gulf of California and/or the west coast of Baja California were routinely assigned to this taxon or to a complex of species confounded under this name (e.g., Haig et al., 1970; Ball and Haig, 1974; McLaughlin, 1975; Snyder-Conn, 1980). Following Haig and McLaughlin's (1991) redescription of *P. lepidus* several species of the complex have been described (i.e., Haig and McLaughlin, 1991; Harvey and McLaughlin, 1991). In the present report three of the species referred to by Haig et al. (1970) as *P. lepidus,* and by Ball and Haig (1974) as *Pagurus* spp., are now described as new species closely allied to, but distinct from, *P. lepidus.*

MATERIALS

Materials for this study have come from the Crustacea collections of the Allan Hancock Foundation (AHF) (now part of the Crustacea collection of the Natural History Museum of Los Angeles County), the National Museum of Natural History, Smithsonian Institution (USNM), and the Natural History Museum of Los Angeles County (LACM). Material formerly belonging to the Allan Hancock Foundation is indicated by an original AHF catalog number in addition to its current LACM number, which follows the AHF number in parentheses. Specimens will be returned to depositories of origin and paratypes also deposited in the Naturhistoriska Riksmuseet, Stockholm (NHRM), Nationaal Natuurhistorisch Museum, Leiden (RMNH), and Muséum National d'Histoire Naturelle, Paris (MNHN). One measurement, shield length (SL), provides an indication of size ranges of the specimens examined.

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SYSTEMATICS

Pagurus rhabdotus new species

Figure 1A–G

Pagurus lepidus: Haig et al., 1970:19 (in part, see remarks); Ball and Haig, 1974:103 (in part, see remarks).

HOLOTYPE. ♂ (SL = 2.4 mm), AHF 6410 (LACM 64-178.1). **Type locality.** Bahía San Hipólito, W. Baja California, Mexico, "Magbay" Expedition, 10–13 m, February 9, 1964, collectors T. Hopkins and T. Scanland.

PARATYPES. W. Baja California, Mexico: Bahía San Hipólito, 2 ♀, 1 ovigerous ♀ (SL = 1.5–2.2 mm), "Magbay" Expedition, 10–13 m, February 9, 1964, collectors T. Hopkins and T. Scanland, AHF 6411 (LACM 64-179.1); outside Punta Hughes, 3 ♂, 2 ♀ (SL = 1.6–2.5 m), "Magbay" Expedition, 20 m, January 30, 1964, collectors T. Hopkins and T. Scanland, USNM 244078, RMNH D 38109, NHRM 4179; Bahía Magdalena, 1 ♂, 1 ♀ (SL = 2.0, 2.2 mm), "Te Vega" station 18-23, 5–7 m, June 2, 1968, collector E. Ball, AHF 6817 (LACM 68-407.1); Bahía Magdalena, 1 ♂ (SL = 2.0 mm), "Te Vega" station 18-23, 3–8 m, June 2, 1968, collectors J. Yarnall and E. Ball, MNHN.

DIAGNOSIS. Shield slightly longer than broad. Ocular peduncles one-half to two-thirds shield length; acicles multispinose. Articles of antennal flagella each with 2 or 3 short setae. Chelipeds unequal, left noticeably smaller. Carpus of right cheliped with row of 3–5 spines on dorsomesial margin. Left chela with dorsomesial face level; ischium usually with row of spinules on ventral margin. Ventral margins of dactyli of ambulatory legs with 6–8 corneous spines; carpi of P_2 with 1 spine on dorsal surface posteriorly. Posterior lobes of telson with simple lateral margins delimited by spine anteriorly, at least on one side. In life, chelae with short, light tan stripes, carpi and meri with brown stripes on white background.

DESCRIPTION. Shield approximately as long as broad, anterior margin between rostrum and lateral projections concave, anterolateral margins sloping or slightly terraced, posterior margin roundly truncate. Rostrum obsolete, unarmed. Lateral projections broadly rounded, unarmed or with very small terminal spinule. Dorsal surface of shield with scattered tufts of setae.

Ocular peduncles one-half to two-thirds shield length, broad basally, corneae slightly dilated. Ocular acicles subrectangular, multispinose (3–5 marginal or submarginal spines); separated basally by approximately one-half basal width of 1 acicle. Interocular lobes weakly developed.

Antennular peduncles overreach ocular peduncles by approximately one-half length of ultimate segment. Ultimate segment with few setae on dorsodistal margin and scattered setae on dorsal and ventral margins. Penultimate segment with few setae ventrally. Basal segment with 1 acute spine on dorsolateral margin distally.

Antennal peduncle only slightly overreaching corneae. Fifth and fourth segments with few tufts of setae. Third segment with small spinule at ventrodistal margin. Second segment with dorsolateral distal angle produced, terminating in acute spine, lateral and mesial margins occasionally with accessory small spine and with long or moderately long setae, dorsomesial distal angle unarmed or with small spine, mesial face with long setae. First segment with small spine on lateral face distally, ventral margin produced and armed with 1 spine laterally. Antennal acicle somewhat arcuate, terminating in small spine, mesial margin with moderately long setae. Antennal flagellum with 2 or 3 short setae or bristles every article.

Right cheliped with dactylus approximately as long as palm, only slightly overlapped by fixed finger and with slight hiatus between dactylus and fixed finger. Cutting edge of dactylus with 1 strong and several small calcareous teeth in proximal half and row of small corneous teeth, interspersed with small calcareous teeth, in distal half, terminating in small corneous claw. Cutting edge of fixed finger with 1 strong calcareous tooth in proximal half, rest of cutting edge with small calcareous teeth, terminating in calcareous tip. Dorsomesial margin of dactylus with row of small, acute spines, dorsal surface slightly elevated in midline and also armed with row of spines and tufts of long, stiff setae, dorsomesial margin and ventral surface with tufts of long, stiff setae. Palm slightly shorter than carpus; dorsomesial margin with row of spines, dorsal surface with irregular rows of small spines, stronger in females, and with numerous tufts of long, stiff setae, fixed finger with irregular row of spines in midline or adjacent to cutting edge, dorsolateral margin with row of small spines often strongest on fixed finger. Carpus slightly longer than merus; dorsomesial and dorsolateral margins each with row of spines (stronger in females), 1 spine on or near distal margin, dorsal surface unarmed but with numerous tufts of long setae, laterodistal margin often with small spine dorsally, lateral and mesial faces with scattered setae, ventrolateral margin with acute spine distally. Merus subtriangular, dorsal margin with few tufts of setae, ventromesial and ventrolateral margins unarmed or with 1 small spine on ventromesial margin and short row of small spines on ventrolateral margin in distal half. Ischium unarmed.

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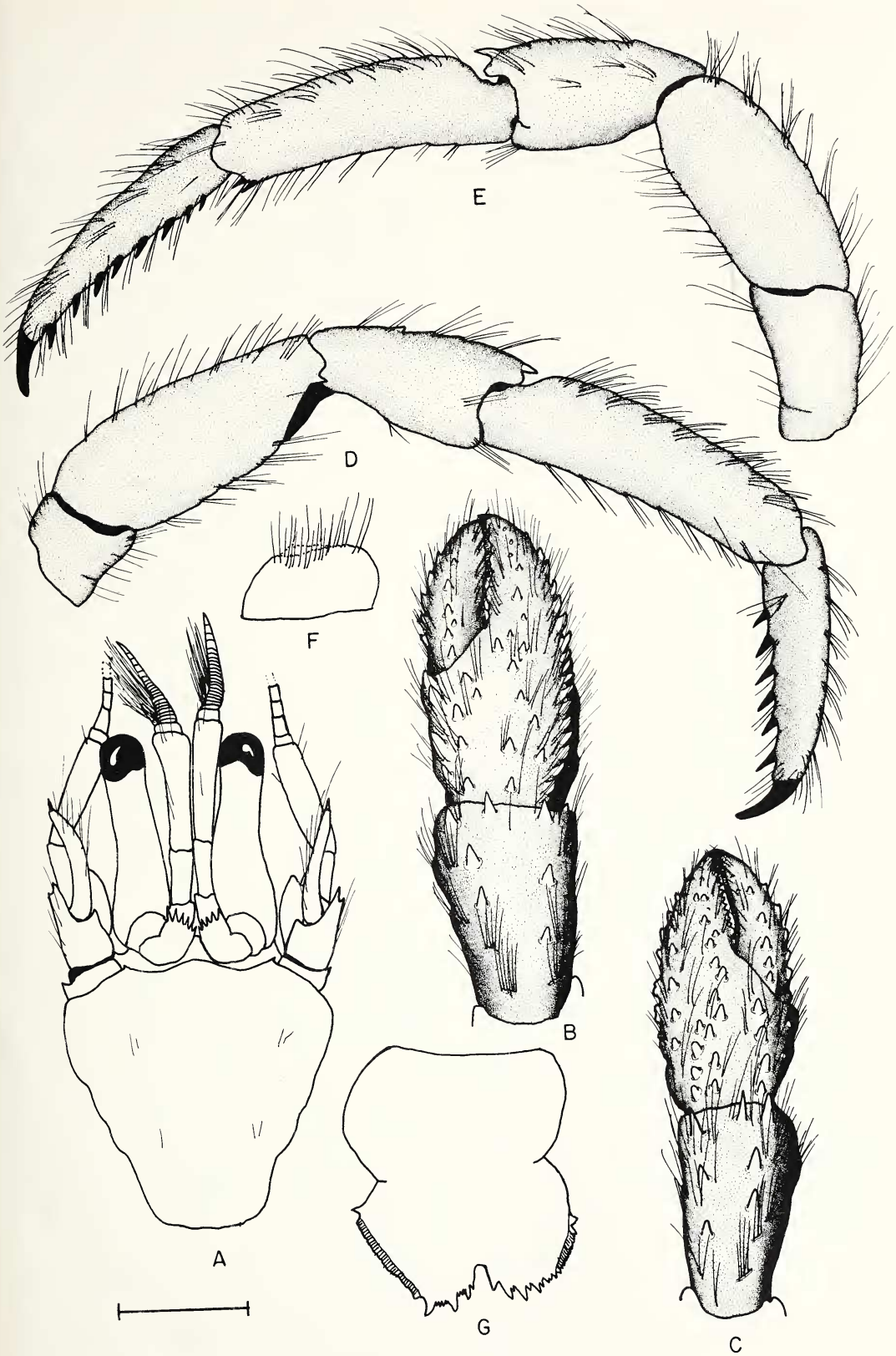
Figure 1. *Pagurus rhabdotus* paratype [AHF 6817 (LACM 68-407.1), Bahía Magdalena, west Baja California, Mexico]: **A,** shield and cephalic appendages; **B,** chela and carpus of right cheliped (dorsal view); **C,** chela and carpus of left cheliped (dorsal view); **D,** right 2nd pereopod (lateral view); **E,** left 3rd pereopod (lateral view); **F,** anterior lobe of sternite of 3rd pereopods; **G,** telson. Scale equals 1.0 mm (A–E) and 0.5 mm (F, G).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Left cheliped with dactylus and fixed finger somewhat spoon-shaped. Dactylus one-fourth to one-third longer than palm; cutting edge with row of corneous teeth, terminating in corneous claw, dorsal surface with row of stiff setae near cutting edge, second row of longer setae in midline accompanied by row of spines, and with row of spines on dorsomesial margin, mesial face and ventral surface also with tufts of long setae. Palm approximately two-thirds length of carpus; elevated in midline, and armed with irregular double row of spines, extending onto the fixed finger as single row, dorsolateral face strongly sloping ventrally, with row of spines and tufts of setae in ventral half and second row of spines and tufts of long setae marginally, dorsomesial face level, dorsomesial margin with row moderate to strong spines and tufts of setae, mesial face with low, sometimes spinulose protuberances and tufts of setae. Carpus usually equaling merus in length, dorsomesial and dorsolateral margins each with row of strong spines and tufts of long setae, dorsodistal margin with 1 strong spine, laterodistal margin usually with small spine, dorsal surface and mesial and lateral faces with scattered setae, ventrolateral margin with 1–3 low protuberances or small spines. Merus triangular, dorsal margin with tufts of setae, ventrolateral margin with row of acute spines in distal half, ventromesial margin with row of spines (only on proximal half in large males), ventral surface with long setae. Ischium frequently with row of spinules on ventral margin.

Second and 3rd pereopods similar. Dactyli slightly less to slightly more than one-half length of propodi (often shortest on left 3rd), moderately broad, terminating in strong, curved corneous claw; dorsal, mesial, and lateral surfaces all with tufts of moderate to long setae, ventral margins each with row of 6–8 corneous spines and long, stiff setae. Propodi exceeding length of carpi by one-third to one-half own length, dorsal surfaces with tufts of long, stiff setae, ventral surfaces each with pair of corneous spines at distal margin (2nd) and usually paired 1st, followed by row of 3–5 widely spaced corneous spines in distal half (3rd). Carpi approximately equaling length of meri; dorsodistal margins each with 1 small spine, dorsal surfaces usually with 1 small spine proximally (2nd), or low protuberances (3rd), and with tufts of long setae, mesial and lateral faces and ventral surface with scattered setae. Meri with tufts of long setae on dorsal margins, ventral margins usually with 1 spine (2nd) and low, sometimes spinulose protuberances (2nd and 3rd) and tufts of long setae, ventrolateral margins each with acute spine distally. Ischia with row of long setae on ventral margins.

Anterior lobe of sternite of 3rd pereopods subrectangular to subsemicircular, unarmed. Fourth pereopods with long dactyli, small preungual process at base of claw; propodal rasp of 4–6 rows of corneous scales; dorsal margins of dactyli, propodi, carpi, and meri (distally) with very long, moderately dense setae.

Exopod of left uropod with row of thick setae on inner margin. Telson with posterior lobes subquadrate, terminal margins slightly oblique, each armed with row of spines, 1 or 2 usually stronger; lateral margins with narrow plate delimited anteriorly by small spine, at least on one side.

COLOR. Antennal flagellum with 3 or 4 brown articles alternating with transparent article. Shield mottled tan and olive drab with reddish rostral region. Ocular peduncles brown on transparent background in median half and olive drab proximally; corneae brown with flecks of gold. Antennular peduncles with white chromatophores dorsally near distal margin of ultimate segment with olive drab on transparent background over all. Antennal peduncles olive drab. Chelipeds with brown patches laterally or mesially on dactyli and fixed fingers, palms with light tan short stripes; carpi and meri with brown longitudinal stripes on white background, ambulatory legs with white distally on dactyli and short, longitudinal brown stripes on white background proximally; propodi, carpi and meri with brown longitudinal stripes on white background (E. Ball field notes).

DISTRIBUTION. Outer coast of Baja California peninsula, Mexico; 2–20 m.

AFFINITIES. Among the Pacific *provenzanoi*-group species, *P. rhabdotus* is one of four species characterized by a delimiting lateral telsonal spine. Although these species are superficially quite similar, the level dorsomesial surface of the palm of the left chela immediately distinguishes *P. rhabdotus* from *Pagurus redondoensis* Wicksten, a species in which this surface is strongly sloped. *Pagurus vetaultae* Harvey and McLaughlin and *Pagurus nanodes*, n. sp., the other species of the quartet, also can usually be distinguished by the slope of this surface of the left chela; however, representatives of both of these species have been observed to have only a moderate slope that could result in a misidentification if this were the only character considered. *Pagurus rhabdotus* may also be distinguished from *P. redondoensis* and *P. vetaultae* by the presence of 1 or more posterior spines on the dorsal surfaces of the carpi of the first pair of ambulatory legs, and by the usually spinose ischium of the left cheliped; however, these characters will not always distinguish *P. rhabdotus* from *P. nanodes*. The longer antennal flagella with only short setae on the articles, the usually more numerous spines on the ventral margins of the dactyli of the ambulatory legs, and larger size at maturity aid in distinguishing *P. rhabdotus* from *P. nanodes* (also see affinities under the latter species). *Pagurus rhabdotus* is also closely allied to *P. lepidus* (Bouvier). Both are distinguished from other related species by the level dorsomesial face of the left chela. However, as previously indicated, the lateral telson plates are delimited anteriorly by a spine, at least on one side, in *P. rhabdotus*. No such spine is present in *P. lepidus*.

In life, the distinctive tan to brown stripes on the

dorsal surfaces of the segments of the chelipeds serve to distinguish *P. rhabdotus* from *P. lepidus* with its generally greenish brown overall color set off by white spines often tinged with red-brown. However, a similar pattern of striping on the chelipeds is also seen in *P. vetaultae,* although the stripes in the latter species are darker, broader, and more diffuse. Differences in the color patterns of the ocular peduncles may aid in rapid field separation. In *P. rhabdotus* the ocular peduncles are brown medially on a transparent background and olive drab proximally, whereas those of *P. vetaultae* are opaque with flecks of red and a white ring at the base of the cornea. The proximal band of color on the dactyli of the ambulatory legs in *P. redondoensis* and *P. nanodes* will also distinguish these species from *P. rhabdotus,* in which longitudinal brown stripes overlie the basic white of these appendages.

ETYMOLOGY. From the Greek *rhabdotus* meaning striped.

REMARKS. *Pagurus rhabdotus* is superficially very similar to *P. lepidus* and has been mistakenly identified as the latter in earlier reports (Haig et al., 1970; Ball and Haig, 1974). Although several taxa had been recognized among the collections of the Allan Hancock Foundation, it was not until we were able to precisely define *P. lepidus* (Haig and McLaughlin, 1991) that correct species assignments could be made.

Pagurus virgulatus new species

Figure 2A–G

Pagurus sp. (*miamensis* group): Ball and Haig, 1974:102 (in part, see remarks).

HOLOTYPE. ♂ (SL = 2.5 mm), AHF 3516 (LACM 35-188.1). **Type locality.** Puerto Parker, Costa Rica, "Velero III" station 468-35, 9 m, February 9, 1935.

PARATYPES. Mexico: El Morro, Bahía de Acapulco, 2 ♂ (SL = 1.2, 1.7 mm), "Te Vega" station 18-21, 6–9 m, May 23, 1968, collector E. Ball, AHF 6821 (LACM 68-409.1). Costa Rica: Bahía Brasilito, 1 ovigerous ♀ (SL = 1.2 mm), "Te Vega" station 18-18, 4.5 m, May 13, 1968, collector E. Ball, AHF 6820 (LACM 68-410.1); Puerto Parker, 3 ♂, 1 ovigerous ♀ (SL = 1.2–2.1 mm), "Velero III" station 467-35, 3.6 m, February 9, 1935, USNM 244079, RMNH D 38110, NHRM 4180. Cocos Island: SW of Isla Pajara, Bahía Weston, 1 ♂ (SL = 1.7 mm), 9–15 m, April 27, 1988, LACM 88-23.1; Bajo Alcyone, 1 ♂ (SL = 1.3 mm), 35 m, March 27, 1989, collector K. Kaiser, LACM 89-179.1. Colombia: Off Isla Gorgona, 1 ♂ (SL = 1.5 mm), "Velero III" station 224-34, 18 m, February 12, 1934, MNHN. Ecuador: Atacames Reef, 2 ♂ (SL = 0.9, 1.2 mm), "Te Vega" station 18-8, 8 m, April 23, 1968, collectors M. Youngbluth and P. Smith, AHF 682 (LACM 68-411.1).

DIAGNOSIS. Shield longer than broad. Ocular peduncles three-fourths to five-sixths shield length; acicles multispinose. Articles of antennal flagella each with 1–3 short setae. Chelipeds unequal, left noticeably smaller. Carpus of right cheliped with 4 or 5 spines on dorsomesial margin. Left cheliped with dorsomesial face of palm strongly sloping; ischium with few spinules on ventral margin. Dactyli of ambulatory legs each with 6–9 corneous spines on ventral margins. Posterior lobes of telson with simple lateral margins, no delimiting spine anteriorly. In life, chelipeds with splotches or stripes of brown; ambulatory legs with longitudinal brown stripe on mesial and lateral faces of carpi and meri, short brown stripe dorsally on propodi and short dorsolateral and dorsoventral stripes on dactyli.

DESCRIPTION. Shield longer than broad, anterior margin between rostrum and lateral projections concave, anterolateral margins sloping or slightly terraced, posterior margin roundly truncate. Rostrum rounded or obsolete, unarmed. Lateral projections subtriangular to broadly rounded, unarmed or with very small terminal spinule. Dorsal surface of shield with scattered tufts of setae.

Ocular peduncles three-fourths to five-sixths shield length, slightly broadened basally and moderately slender distally, cornea slightly dilated. Ocular acicles subrectangular, multispinose (3–5 widely spaced marginal or submarginal spines); separated basally by approximately one-half basal width of 1 acicle. Interocular lobes weakly developed.

Antennular peduncles overreach ocular peduncles by approximately one-eighth to one-fourth length of ultimate segment. Ultimate and penultimate segments with few scattered setae. Basal segment with 1 acute spine on dorsolateral margin distally.

Antennal peduncle only slightly overreaching corneae. Fifth and fourth segments with few tufts of setae. Third segment unarmed or with very small spinule at ventrodistal margin. Second segment with dorsolateral distal angle produced, terminating in acute spine, lateral and mesial margins with long or moderately long setae, dorsomesial distal angle unarmed or with small spine, mesial face with long setae. First segment with small spine on lateral face distally (small individuals), ventral margin produced and armed with 1 spine laterally. Antennal acicle somewhat arcuate, terminating in small spine, mesial margin with moderately long setae. Antennal flagellum with 1–3 short setae or bristles every article.

Right cheliped with dactylus approximately as long as palm, slightly overlapped by fixed finger. Hiatus between dactylus and fixed finger. Cutting edge of dactylus with 1 strong and several small calcareous teeth in proximal half and row of small corneous teeth distally, terminating in small corneous claw. Cutting edge of fixed finger with 1 strong calcareous tooth in proximal half, rest of cutting edge with small calcareous teeth, also terminating in corneous claw. Dorsomesial margin of dactylus with row of small acute or blunt spines, dorsal surface slightly elevated in midline and also armed with row of small spines and tufts of long, stiff setae, dorsomesial margin and ventral surface with tufts of long, stiff setae. Palm slightly shorter than carpus; dorsomesial margin with row of spines,

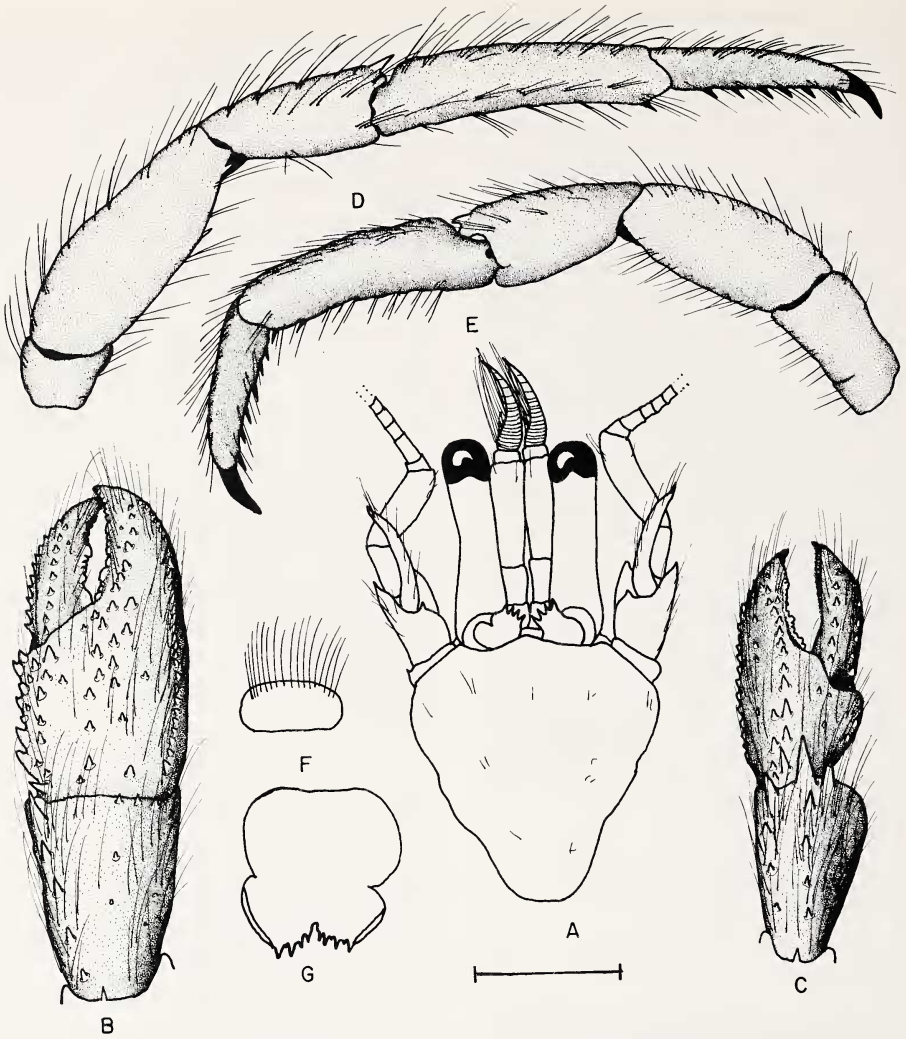


Figure 2. *Pagurus virgulatus* paratype [LACM 88-23.1, Bahía Weston, Cocos Island]: **A**, shield and cephalic appendages; **B**, chela and carpus of right cheliped (dorsal view); **C**, chela and carpus of left cheliped (dorsal view); **D**, right 2nd pereopod (lateral view); **E**, left 3rd pereopod (lateral view); **F**, anterior lobe of sternite of 3rd pereopods; **G**, telson. Scale equals 1.0 mm (A–E) and 0.5 mm (F, G).

dorsal surface with several irregular rows of small spines and tufts of long setae, also with row of spines and few additional scattered spinules on fixed finger, dorsolateral margin with row of small spines extending length of fixed finger. Carpus slightly longer than merus; dorsomesial margin with row of 4 or 5 rather widely spaced spines strongest distally, 1–3 spines on or near distal margin and frequently additional row of spines laterad of midline, dorsal surface also with numerous tufts of long setae, dorsolateral margin not delimited, lateral and mesial faces with low protuberances and tufts of setae. Merus subtriangular, dorsal margin with few setae, ventromesial and ventrolateral margins unarmed or with 1–3 spines distally, distal margin sometimes with acute spine. Ischium unarmed or with small spine at ventrolateral distal angle.

Left cheliped with dactylus and fixed finger somewhat spoon-shaped. Dactylus slightly longer than palm; cutting edge with row of corneous teeth, terminating in corneous claw, dorsal surface with row of spines and stiff setae, mesial margin with row of low, spinulose protuberances and long setae, ventral surface also with tufts of long setae. Palm slightly more than half length of carpus; elevated in midline, often into prominent crest, and armed with irregular double row of spines, extending onto fixed finger as single row adjacent to cutting edge, dorsolateral face strongly sloping ventrally, with longitudinal row of widely spaced small spines or only row of setae in ventral half, margin with row of spines and tufts of long setae, dorsomesial face also usually strongly sloping, armed with few scattered spines and tufts of long setae, dorsomesial

margin not delimited. Carpus approximately equaling merus in length; dorsomesial and dorsolateral margins each with row of strong, acute spines and tufts of long setae, dorsodistal margin with 1 strong spine, dorsal surface and mesial and lateral faces with scattered setae, ventrolateral margin with 1 strong spine distally. Merus triangular, dorsal margin with row of long setae and often acute spine on distal margin, ventrolateral and ventromesial margins each with row of acute spines and long setae. Ischium with few minute spinules on ventral margin.

Second and 3rd pereopods similar. Dactyli one-half to two-thirds length of propodi, 3rd dactyl usually moderately broad, terminating in strong, curved corneous claws; dorsal, mesial, and lateral surfaces all with tufts of moderate to long setae, ventral margins each with row of 6–9 corneous spines and long, stiff setae. Propodi exceeding length of carpi by one-third to one-half own length, dorsal surfaces with tufts of long, stiff setae, ventral surfaces each with 1 or 2 corneous spines at distal margin (2nd) and 1 additional spine in distal third of segment (3rd). Carpi two-thirds to three-fourths length of meri; dorsodistal margins each with 1 small spine, dorsal surfaces with tufts of long setae, mesial and lateral faces and ventral surface with scattered setae. Meri with long setae on dorsal margins, ventromesial or ventrolateral (2nd) margin usually with 1 to several spines distally and tufts of long setae. Ischia with row of long setae on ventral margins.

Anterior lobe of sternite of 3rd pereopods subrectangular to subquadrate, unarmed. Fourth pereopods with moderately long dactyli, small preungual process at base of claw; propodal rasp of 4 or 5 rows of corneous scales; dorsal margins of dactyli, propodi, carpi, and meri (distally) with tufts of long setae.

Exopod of left uropod with row of thick setae on inner margin. Telson with subtriangular posterior lobes; terminal margins usually oblique, each armed with row of spines, 1 or 2 sometimes stronger; lateral margins with simple narrow plate, no anterior spine.

COLOR. Antennal flagellum banded with brown spots (2 or 3 articles) interspersed with white (1 or 2 articles). Shield off-white with few brown patches. Ocular peduncles off-white or white with hints of brown; corneae black or black with flecks of gold. Antennules white with hint of blue or uniformly off-white. Antennal peduncles off-white; antennal acicle with patches of brown. Chelipeds off-white with splotches (smaller individuals) or with brown stripes on white background. Ambulatory legs with short brown stripes on white background dorsally on propodi, carpi, and meri and long, longitudinal stripe on lateral and mesial faces; dactyli with short dorsolateral and ventrolateral stripes proximally (E. Ball field notes).

DISTRIBUTION. Acapulco, Mexico to Ecuador; Cocos Island; 5–40 m.

AFFINITIES. *Pagurus virgulatus* is most closely allied to *Pagurus arenisaxatilis* Harvey and McLaughlin, a species apparently endemic to the Gulf of California, Mexico. The two species are distinguished by the armature of the carpus of the right cheliped and ventral margins of the dactyli of the ambulatory legs, and by the setation of the antennal flagella. *Pagurus virgulatus* has only 4 or 5 rather widely spaced spines on the dorsomesial margin of the carpus of the right cheliped, whereas an irregular, often distally double row of 7–10 spines is present on this margin in *P. arenisaxatilis*. The ventral margins of the dactyli of the ambulatory legs are armed with 5–8 corneous spines, and the articles of the antennal flagella are provided with only 1–3 short setae or bristles in *P. virgulatus*. In *P. arenisaxatilis* the dactyli of the ambulatory legs are armed with 7–13 corneous spines and the articles of the antennal flagella have both long and short setae, at least in the proximal half. In living specimens, the color patterns of the two species provide reliable distinctions. Although these two species, like most others of the Pacific *provenzanoi* group, have striped ambulatory legs, the chelipeds of *P. virgulatus* are splotched with brown in small individuals or have brown stripes on a white background. The chelipeds of *P. arenisaxatilis* are generally solidly colored olive or tan, with the distal halves of the dactyli and fixed fingers white.

ETYMOLOGY. From the Latin *virgulatus*, meaning striped and referring to the color patterns of the chelipeds and ambulatory legs.

REMARKS. Ball and Haig (1974) referred to three undescribed species as *Pagurus* spp. (*miamensis* group) [*miamensis* being an earlier name for the *provenzanoi* group of *Pagurus* species; see McLaughlin, 1975]. Of these specimens, three lots from Mexico, Costa Rica, and Ecuador represent *P. virgulatus*.

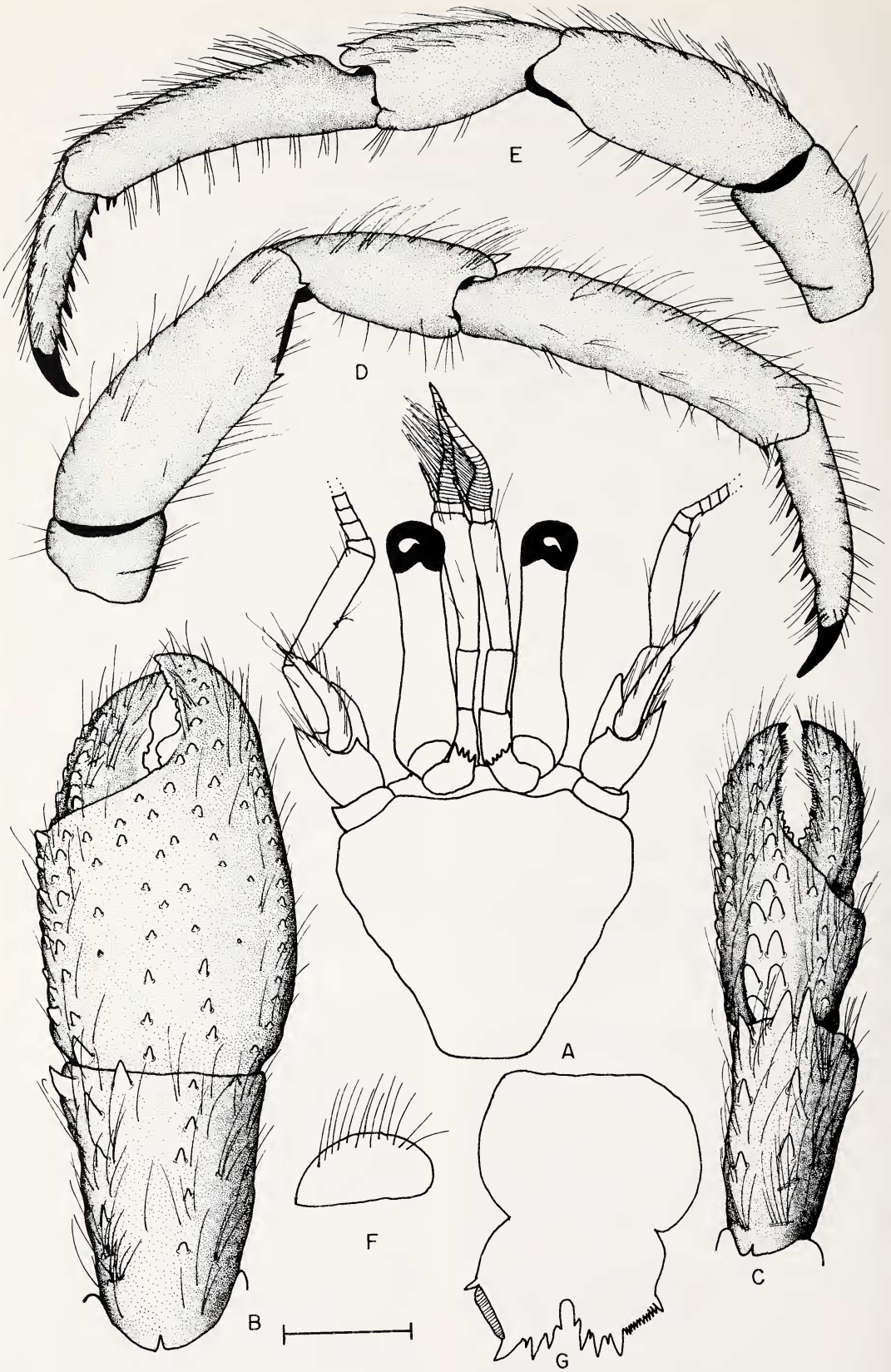
Pagurus nanodes new species

Figure 3A–G

Pagurus spp. (*miamensis* group): Ball and Haig, 1974:102 (in part, see remarks).

HOLOTYPE. ♂ (SL = 2.0 mm), AHF 681 (LACM 68-412.1). **Type locality.** Punta Paitilla, Panama, "Te Vega" station 18-14b, 1.8 m, May 6, 1968, collector E. Ball.

PARATYPES. Costa Rica: Bahía Brasilito, 3 ♂ (SL = 1.3–1.4 mm), "Te Vega" station 18-18, 4.5 m, May 13, 1968, collector E. Ball, AHF 6826 (LACM 68-413.1); near Puntarenas, 2 ♂ (SL = 0.9, 1.1 mm), "Te Vega" station 18-17c, intertidal, May 11, 1968, collectors L. Eickstaedt and E. Ball, AHF 6825 (LACM 68-414.1). Panama: Punta Paitilla, 4 ♂, 2 ovigerous ♀ (SL = 1.6–2.0 mm), "Te Vega" station 18-14b, 1.8 m, May 6, 1968, collector E. Ball, AHF 6822 (LACM 68-415.1); Isla Naos, 1 ovigerous ♀ (SL = 0.9 mm), "Te Vega" station 18-14a, 1.5–3 m, May 5, 1968, collector E. Ball, AHF 6824 (LACM 68-416.1); Isla Taboguilla, 1 ovigerous ♀ (SL = 1.8 mm), "Albatross," 1.8 m, October 31, 1904, USNM; W side Isla Taboguilla, 9 ♂, 4 ♀, 21 ovigerous ♀, 2 juveniles (SL = 1.0–1.8 mm), LGA station 57, 2 m, April 7, 1969, collectors L.G. Abele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and A. Rodaniche, USNM 244089; same locality, 1 ovigerous ♀, 1 juvenile (SL = 0.8, 1.2 mm), LGA station 93, 2 m, April 7, 1969, collectors L.G. Abele and A. Rodaniche, USNM 244092; same locality, 4 ♂, 2 ovigerous ♀, 2 juveniles (SL = 0.9–1.8 mm), LGA station 59, 2 m, April 11, 1969, collectors L.G. Abele, A. Rodaniche, and J. Graham, USNM 244090; Taboga, 37 ♂, 6 ♀, 16 ovigerous ♀ (SL = 0.8–2.4 mm), intertidal, December 24, 1990, collector J. Crain, USNM; Isla Culebra, 1 ♂, 1 ovigerous ♀ (SL = 1.7, 2.2 mm), intertidal, December 20–21, 1990, collector J. Crain, USNM; Panama Bay, 12 ♂, 7 ♀, 5 ovigerous ♀ (SL = 0.7–1.2 mm), December 11, 1981, collector T. Spight, AHF 8112 (LACM 81-130.1), MNHN; Panama Bay, 5 ♂, 1 ♀ (SL = 1.2–1.7 mm), ? 1981, collector T. Spight, RMNH D 38108, NHRM 4178; Pacific Panama, 3 ♂ (SL = 1.7–2.2 mm), 1976, collector P. Abrams, AHF 7616 (LACM 76-627.1). Ecuador: Isla de Santa Clara, Gulf of Guayaquil, 2 ovigerous ♀ (SL = 1.4, 2.0 mm), "Te Vega" station 18-1, 7.5 m, April 6, 1968, collectors Ball, Yarnall, Youngbluth and Smith, AHF 6823 (LACM 68-417.1).

DIAGNOSIS. Shield longer than broad. Ocular peduncles one-half to three-fourths shield length; acicles multispinose. Articles of antennal flagella each with 2–4 short and usually 1 or 2 longer setae. Chelipeds unequal, left noticeably smaller. Carpus of right cheliped with row of widely spaced spines on dorsomesial margin. Left cheliped with dorsomesial face of palm moderately to strongly sloped; ischium unarmed. Dactyli of ambulatory legs each with 5–7 corneous spines on ventral margins. Posterior lobes of telson with simple to denticulate lateral plates delimited anteriorly by strong spine. In life, chelipeds with distally white or light orange dactyli and fixed fingers; ambulatory legs with proximal band of brown (dactyli), distal band of blue (propodi and meri), carpi brown or orange.

DESCRIPTION. Shield usually longer than broad, appreciably so in small individuals, anterior margin between rostrum and lateral projections concave, anterolateral margins sloping, posterior margin roundly truncate. Rostrum obsolete, unarmed. Lateral projections broadly rounded, unarmed, or with very small terminal spinule. Dorsal surface of shield often with scattered tufts of setae.

Ocular peduncles one-half to three-fourths shield length, broad basally and tapering to base of slightly dilated corneae. Ocular acicles subrectangular, multispinose (3–6 marginal or submarginal spines); separated basally by one-half to entire basal width of 1 acicle. Interocular lobes weakly developed.

Antennular peduncles overreach ocular peduncles by one-fourth to one-half length of ultimate segment. Ultimate segment with few setae on dorsodistal margin and scattered setae on dorsal and ventral margins. Penultimate segment with few setae ventrally. Basal segment with 1 acute spine on dorsolateral margin.

Antennal peduncle overreaching corneae by one-fourth to one-half length of ultimate segment. Fifth and fourth segments with few tufts of setae. Third segment unarmed or with very small spinule at ventrodistal margin. Second segment with dorsolateral distal angle produced, terminating in acute spine, lateral margin often with accessory spine, mesial margin with long or moderately long setae, dorsomesial distal angle unarmed or with small spine, mesial face with long setae. First segment occasionally with small spine on lateral face distally, ventral margin produced and armed with 1 spine laterally. Antennal acicle somewhat arcuate, terminating in small spine, mesial margin with moderately long setae. Antennal flagellum with 2–4 short setae or bristles and often 1 or 2 longer setae every article.

Right cheliped exhibiting marked sexual dimorphism in large males. Dactylus shorter than to approximately as long as palm, overlapped by fixed finger. Slight to prominent hiatus between dactylus and fixed finger. Cutting edge of dactylus with 1 strong and several small calcareous teeth in proximal half and row of small corneous teeth, interspersed with small calcareous teeth, in distal half or only calcareous teeth (large males), terminating in small corneous or calcareous claw. Cutting edge of fixed finger often with few calcareous teeth proximally and row of corneous teeth distally, terminating in corneous or calcareous tip. Dorsomesial margin of dactylus with row of small acute or blunt spines, dorsal surface slightly elevated in midline, sometimes forming prominent crest, and also armed with row of small spines and tufts of long, stiff setae, dorsomesial and ventromesial margins and ventral surface with tufts of long, stiff setae in large (>2.0 mm) males, but often with row of spinulose protuberances on ventromesial margin in small individuals. Palm equaling or somewhat shorter than carpus; dorsomesial margin with single or double row of spines, strongest in small specimens, dorsal surface with numerous tufts of long setae and small spines in irregular rows or scattered distally, row of small spines on fixed finger adjacent to cutting edge, dorsolateral margin with low protuberances proximally becoming row of small spines on fixed finger (large males) or row of strong spines (small males and females). Carpus slightly longer than merus, dorsomesial margin with row of rather widely spaced spines, and 1 or 2 stronger spines on or near distal margin, dorsal surface with row of spines

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Figure 3. *Pagurus nanodes* paratype [AHF 7616 (LACM 76-627.1), Pacific Panama]: **A**, shield and cephalic appendages; **B**, chela and carpus of right cheliped (dorsal view); **C**, chela and carpus of left cheliped (dorsal view); **D**, right 2nd pereopod (lateral view); **E**, left 3rd pereopod (lateral view); **F**, anterior lobe of sternite of 3rd pereopods; **G**, telson. Scale equals 1.0 mm (A–E) and 0.5 mm (F, G).

laterad of midline, decreasing in strength with increased size of individuals, and with numerous long setae, dorsolateral margin not clearly delimited, lateral and mesial faces with scattered setae, ventrolateral margin with acute spine distally. Merus subtriangular, dorsal margin with few tufts of setae, distal margin often with 1 spine, ventromesial margin unarmed or with 1 or 2 blunt spines, ventrolateral margin with 1–4 acute spines. Ischium unarmed.

Left cheliped with dactylus and fixed finger somewhat spoon-shaped. Dactylus slightly longer than palm. Cutting edge often with few calcareous teeth proximally and row of corneous teeth distally, terminating in corneous claw, dorsal surface with row of stiff setae near cutting edge, second row of longer setae and row of small spines in midline, dorsomesial margin with row of low protuberances or small spines and tufts of long setae, ventral surface also with tufts of long setae. Palm approximately two-thirds length of carpus; slightly elevated in midline and armed with irregular double row of spines, extending onto fixed finger as single row adjacent to cutting edge, dorsolateral face strongly sloping ventrally, with row of small spines in ventral half and second row of protuberances or spines and tufts of long setae marginally, dorsomesial face with moderate to strong slope, dorsomesial margin delimited by row of low, spinulose protuberances or moderate to strong spines (small individuals) and tufts of setae, mesial face with low protuberances and tufts of setae. Carpus usually equaling or slightly longer than merus; dorsomesial and dorsolateral margins each with row of strong spines and tufts of long setae, dorsodistal margin with 1 strong spine, dorsal surface and mesial and lateral faces with scattered setae, laterodistal margin usually with acute spine dorsally and 1 acute spine on ventrolateral margin distally. Merus triangular, dorsal margin with tufts of setae, distal margin often with 1 spine, ventrolateral margin with row of acute spines in distal half, ventromesial margin also with row of acute spines, ventral surface with long setae. Ischium unarmed.

Second and 3rd pereopods similar. Dactyli slightly less to slightly more than one-half length of propodi, moderately broad, terminating in strong, curved corneous claws; dorsal, mesial, and lateral surfaces all with tufts of moderate to long setae, ventral margins each with row of 5–7 corneous spines and long, stiff setae. Propodi exceeding length of carpi by one-fourth to one-third own length, dorsal surfaces with tufts of long setae, ventral surfaces each with 1 or 2 corneous spines at distal margin (2nd) or paired 1st and usually 1 additional spine in distal third of segment (3rd). Carpi equaling or slightly shorter than meri; dorsodistal margins each with 1 spine, dorsal surfaces with tufts of long setae, mesial and lateral faces and ventral surface with scattered setae. Meri with tufts of long setae on dorsal and ventral margins, ventrolateral distal angle with acute spine and ventrolateral margin with acute spine distally (2nd) or unarmed (3rd). Ischia with row of long setae on ventral margins.

Anterior lobe of sternite of 3rd pereopods subrectangular to semisubcircular, unarmed. Fourth pereopods with long dactyli, small preungual process at base of claw; propodal rasp of 4–6 rows of corneous scales; dorsal margins of dactyli, propodi, carpi, and meri (distally) with very long, dense setae.

Exopod of left uropod with row of thick setae on inner margin. Telson with posterior lobes subtriangular; terminal margins oblique, each armed with row of spines, 2–4 stronger; lateral margins with narrow, simple, or denticulate plate delimited by strong spine.

COLOR. Antennal flagellum with brown (or red) and white articles alternating (4 brown, 1 white). Shield white with hints of orange. Ocular peduncles with numerous small red chromatophores on off-white background; corneae black with patches of gold. Antennules off-white with brown stripe distally on ultimate and penultimate segments. Right cheliped with distal halves of dactylus and fixed finger white, palm mottled brown and white; carpus brown laterally and white, shading to orange mesially; merus brown with bright blue band at distal margin. Left cheliped with dactylus and fixed finger pale orange to white, palm mottled brown and white; carpus brown on mesial and lateral faces, orange grading to white dorsally; merus dark brown with bright blue band at distal margin. Ambulatory legs with dactyli pale orange in distal half and dark brown band proximally; propodi with bright blue band at distal margin, pale orange grading to white in following distal half, brown in proximal half; carpi brown; meri with bright blue band at distal margin, with orange in remaining distal half, proximal half white with hints of pale brown (E. Ball field notes).

DISTRIBUTION. Costa Rica to Ecuador; intertidal to 3.5 m.

AFFINITIES. *Pagurus nanodes* appears to be most closely related in morphology to *P. redondoensis* Wicksten and *P. vetaultae* Harvey and McLaughlin. In life it is readily distinguished from all other eastern Pacific *provenzanoi*-group representatives by its distinctive color patterns, most notably bands rather than longitudinal stripes of color on the propodi of the ambulatory legs and solidly colored (orange) carpi. In preserved material where color patterns have faded, it is best distinguished from both *P. redondoensis* and *P. vetaultae* by the fewer spines (5–7) on the ventral margins of the dactyli of the ambulatory legs. Specimens of *P. nanodes* in which the dorsomesial margin of the left chela exhibits only a moderate slope might be confused with specimens of *P. rhabdotus*. The short antennal flagella, with more setose articles, immediately distinguish *P. nanodes*, as does its extremely small size. Females of this species are ovigerous at shield lengths between 0.9 and 1.4 mm.

ETYMOLOGY. The specific name is from the Greek *nanodes,* meaning small or dwarfish.

REMARKS. Numerous specimens from Ecuador, Panama, and Costa Rica cited by Ball and Haig (1974) as *Pagurus* spp. (*miamensis* group), and some of the specimens from Panamanian *Pocillopora* habitats cited by Abele (1972) as an undescribed species of *Pagurus* have proved to be *P. nanodes.*

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